

LIFE-HISTORY AND BIOLOGY OF THE OYSTER CRAB, *PINNOTHERES OSTREUM* SAY

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While the adult female of several species of the pea crab, *Pinnotheres*, has been known since ancient times, it is not clear when the first male was observed and described. The earliest reference available to the present authors was found in a paper by Thompson (1835).

He describes the male of *P. pisum* as being firm in texture, with compressed, hairy appendages and of flatter form and much smaller size than the (adult) globular, soft-shelled female. Such hard-shelled *P. pisum* were generally all thought to be males until Orton (1921) demonstrated the existence of hard-shelled females, which except for differences in the genital apertures and the pleopods proved to be indistinguishable from the males. However, hard-shelled females were known in at least four other species of *Pinnotheres* prior to 1921 (Rathbun, 1918). Possibly, Thompson (1835) was also aware of this in *P. pisum* as he states, "For a considerable time the young females are scarcely to be distinguished from the males, and in this stage both differ so much from the adult, as to render it probable that they have often been taken for individuals of different species, . . ."

Orton (1921) was the first to find a soft-shelled male, which except for the same characteristics as mentioned above resembled the immature female of similar size.

A few years later, Atkins (1926) studied and described all the growth stages of *P. pisum* found in *Mytilus edulis* in English waters. As Orton, she regarded the hard-shelled crabs as free-living, invasive crabs, a point of view which the author later abandoned (Atkins, 1954, 1955). Hence the hard-shelled stage of both sexes was designated as Stage I. In the female, four more stages were described, the fifth and last stage being the mature crab. In the male, only the hard-shelled stage was described, no reference being made to Orton's discovery of a soft-shelled specimen. It was stated, however, that a few abnormal males were found. Soft-shelled males were found also by Mercier and Poisson (1929), who stated that they were abnormal due to the influence of an entoniscid parasite. Later Atkins (1933) disproved this statement and expressed the hope of discussing the matter in a later paper as she still considers these males as abnormal.

Stauber (1945) found and described similar growth stages in *P. ostreum* from the American oyster, *Crassostrea virginica*. He therefore followed Atkins (1926) in designating the hard-shelled stage as the first (invasive) stage, which in the female is succeeded by four more stages as in *P. pisum*. Stauber also found a number of soft-shelled males, evidently corresponding with the finds of *P. pisum* mentioned above. With some reservation, he referred these males to a second stage

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following the hard-shelled stage. This hypothesis does not agree with the general belief that the hard-shelled male is the adult stage of this sex.

Although numerous species of *Pinnotheres* have been described (Bürger, 1895; Rathbun, 1918; Tesch, 1918; and others), knowledge about post-larval stages, other than the adult, is scarce for all species except the two mentioned above. Only in two species has the first crab stage been described, viz. in *P. taylori* by Hart (1935), and in *P. ostreum* by Sandoz and Hopkins (1947). In both cases the crabs were reared from the egg in the laboratory, and the stage has never been reported from nature.

The latter paper included a description of the early developmental stages of which there proved to be four zoeal stages, of which the first two had been described earlier (Hyman, 1924), and one megalopa. It therefore almost completed our knowledge of the whole developmental cycle in any pea crab for the first time. The authors, however, pointed out that two or more instars were still unknown as the two crabs reared by them measured only about 0.6 mm. in carapace width while the smallest hard-shelled *P. ostreum* found by Stauber (1945) measured 1.4 mm.

Much to our surprise, the missing instars as well as the first crab stage were found in a number of oyster spat collected in Delaware Bay on August 17th in 1955. This meant that the hard-shelled stage could not be the first invasive stage. The fact that hard-stage crabs of several species of *Pinnotheres* have been taken free in the water (Verrill and Smith,² 1874; Rathbun, 1918; Berner, 1952; and others), or trapped between the valves of their host (Orton, 1921; and others), had to be explained otherwise. Two hard-stage oyster crabs were also caught outside their host by the present authors. In addition to the description of the new growth stages, a re-investigation of the biology of *P. ostreum* was therefore decided upon. This seemed especially worth while since Stauber's paper is the only comprehensive work on the biology of any pinnotherid crab. This seems strange considering that the genus *Pinnotheres* alone comprises more than a hundred species, unless, which is very possible, many of them are synonyms. The results of our subsequent studies are the subject of the present paper.

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MATERIALS AND METHODS

The present work on the biology and life-history of *P. ostreum* was carried out at the New Jersey Oyster Research Laboratory, Rutgers University, from August, 1955 to December, 1956.

² Judging by their figure, Pl. I, Fig. 2, the species found was *P. maculatus*, and not *P. ostreum* as stated.

Studies on the rate of growth and development, one of the primary objects, were based on extensive collections in the field. Since such factors as the age and size composition of the host populations, as well as the environmental conditions, could be expected to vary from one area to another, it was important to eliminate as many of these variables as possible. We decided, therefore, to find one or two small grounds in Delaware Bay with a good set of 1955 oyster spat and with a high incidence of infestation with oyster crabs. These grounds were then to be sampled at regular intervals throughout the period of investigation. This procedure enabled us to deal with local populations of oysters and crabs of known year-classes. It also eliminated the risk of dealing with oyster populations exhibiting different incidences of infestation, a factor which later proved to be very important to the interpretation of the assembled data.

One ground was selected at Pierces Point about ten miles north of Cape May Point, and another was selected about two miles west of Pierces Point on the Bay Shore Channel Bed, an area where commercial oyster dredging is prohibited. At Pierces Point, oysters were collected by hand at low water when the oysters were exposed. Here a heavy mortality of the 1955 spat occurred late in the winter of 1955-1956, wherefore sampling was discontinued except for a few samples during the summer of 1956, and sampling of 1956 spat in the fall of that year. On the Bay Shore Channel Bed the depth at mean low water is about 6 meters, and here oysters were obtained from the research vessel "Julius Nelson." Little mortality of the 1955 spat was noted on this ground, but some mortality of the crabs occurred in February and early March of 1956 (Fig. 5).

In addition to the regular collections of crabs from 1955 spat (Table I), other collections, which included crabs from older oysters as well as from 1956 spat, were made on the above mentioned as well as other grounds in Delaware Bay. An effort was made to secure a high number of crabs at each collection. As seen in Table I, the lowest number taken in the series of regular samples was 55, and most of the samples contained more than a hundred crabs. Collections began at a time when most of the 1955 crabs were still in the first crab stage, thus enabling us to study the whole post-planktonic life cycle of the crab.

On the Bay Shore Channel Bed, which constituted our main sampling ground, bottom temperatures were determined with a reversing thermometer on each collecting date.

Oysters brought back to the laboratory were, with few exceptions, examined alive and always under a dissecting microscope. Infested oysters, and from time to time also all of the uninfested oysters collected along with them, were measured to the nearest 0.5 mm. in length with vernier calipers. The crabs were measured under the microscope to the nearest 0.1 mm. in carapace width. The smaller crabs were measured with a calibrated ocular micrometer, while the majority were measured on a millimeter glass ruler or by vernier calipers. The amount of error was judged to be the same for the last two methods, as they were checked on several occasions. Unless otherwise indicated, all crab sizes in the present paper refer to the width of the carapace.

Notes on the general condition, amount of gill damage caused by the crab, and other pertinent data concerning the infested oysters were taken on the majority of the collections.

All of the oyster crabs found, except those used for dissections and experiments,

were preserved in alcohol, and specimens of the new instars have been deposited in the United States National Museum and in the Zoology Museum of the University of Copenhagen, Denmark.

For various reasons it was decided to reserve a detailed description of the new instars and the necessary revision of the numbering of all the post-planktonic growth

TABLE I

Number and mean size for each collection of oysters and oyster crabs of the 1955 year-class taken at Pierces Point and the Bay Shore Channel Bed, with a column showing the incidence of infestation

Date of collection	Number of infested oysters	Mean length of oysters in mm.	Total number of <i>Pinnotheres</i>	Range in carapace width in mm.	Mean carapace width in mm.	Incidence of infestation in per cent
Pierces Point						
17- 9-55	167	13.8	279	0.6- 2.4	0.69	69.0
1-11-55	101	15.4	107	0.7- 2.1	1.35	60.1
5-12-55	175	18.1	185	0.7- 2.2	1.42	56.6
13-12-55	—	—	215	0.6- 2.0	1.31	—
4- 1-56	127	19.2	130	0.7- 2.2	1.46	64.8
25- 1-56	55	17.4	55	0.8- 2.1	1.51	56.1
23- 2-56	98	18.9	99	0.9- 2.5	1.52	56.4
22- 3-56	85	19.2	86	0.8- 2.2	1.50	43.6
7- 7-56	16	30.6	16	2.5- 4.7	3.10	11.7
Bay Shore Channel Bed						
14-12-55	192	—	193	0.6- 3.1	1.54	68.3
6- 1-56	120	19.1	130	0.7- 2.6	1.47	72.8
4- 2-56	134	21.7	139	0.7- 2.7	1.59	72.4
5- 3-56	81	22.5	81	1.0- 2.8	1.75	55.1
18- 4-56	127	22.0	127	0.7- 3.2	1.79	52.9
3- 5-56	124	21.1	124	0.9- 2.6	1.63*	59.9
22- 5-56	96	22.6	96	0.9- 2.7	1.75	58.9
5- 6-56	103	24.9	104	0.8- 2.9	1.95	53.1
14- 6-56	110	25.0	110	1.6- 4.2	2.35	62.5
20- 6-56	100	25.4	100	1.1- 5.8	2.46*	58.1
6- 7-56	116	34.3	124	1.8- 7.8	3.64	41.1
11- 7-56	103	35.7	106	1.8- 7.7	4.03	35.7
18- 7-56	108	39.7	113	2.2- 9.2	5.18	35.0
26- 7-56	118	41.6	119	2.5- 9.6	5.76	33.1
1- 8-56	63	44.8	63	2.8- 8.6	6.24	35.0
16- 8-56	118	43.3	119	2.2- 9.6	6.60	28.9
12- 9-56	114	49.2	114	4.4- 9.8	7.41	33.6
9-10-56	100	51.7	100	5.2-10.0	7.68	34.4

* Measurements from formalin preserved specimens.

stages to a second paper. Consequently the present paper only includes such brief notes on the new instars, as well as the previously described stages, as is necessary to the understanding of the following account of the life-history and biology of the crab.

Laboratory experiments and observations were carried out to a limited extent, and some of the moulting experiments yielded valuable information. Holes were

chipped in the ventral portion of oysters to insert crabs of known stage, sex and size with the hope that moulting might occur. Although only a small percentage of the crabs moulted, the method proved valuable since crabs kept in Petri dishes did not moult at all except in those cases where the crabs were obviously ready to moult on arrival to the laboratory. Oysters for the above purpose were generally collected from the upper parts of the Delaware Bay Natural Seed Beds where the percentage of oysters infested with the oyster crab was very low. Occurrence of moulting inside the oysters could be detected without opening them since the cast exoskeleton is ejected shortly after a moulting has taken place.

GROWTH STAGES IN PINNOTHERES OSTREUM

As indicated earlier, the hard-shelled stage is not the first invasive stage. The true invasive stage is the first crab stage. Proof of this are the following facts: 1. The morphology of the first crab stage shows adaptations both for a free-swimming existence and for entering the host. 2. The first crab stage was found abundantly inside oysters but it was also collected in plankton samples in Delaware Bay. 3. While all subsequent stages were found inside oysters, no earlier stages, such as the megalopa which was suggested by Atkins (1954) to be the invasive stage in *P. pinnotheres*, were ever taken in the host animals.

In the following, therefore, Stauber's (1945) Stage I will be referred to as the *hard stage*. The new instars between the *invasive stage* and the hard stage will be called the *pre-hard stages*, a term which is arbitrarily defined as excluding the invasive stage. To avoid confusion with the earlier literature, and because we have not yet been able to assign pre-hard crabs to definite growth stages, we have adhered to the numbering of the *post-hard stages* as given by Stauber, except for the male in which we found that no post-hard stage exists. In addition to the following remarks, the summary of the main characteristics of all post-planktonic growth stages presented in Table II should be helpful to the reader.

Invasive stage

The mean size of the two crabs reared by Sandoz and Hopkins (1947) was 0.59 mm. while the mean of 183 specimens collected by us at Pierces Point on September 17, 1955 was 0.65 mm. with a size range from 0.59 to 0.73 mm.

The invasive stage is similar to the hard stage in many respects, which is remarkable considering that the pre-hard instars separating these two stages in the developmental cycle have a very different morphology. Both of these stages have a flat carapace, flattened pereopods with thickened posterior borders, and long, plumose swimming hairs on the third and fourth pairs. They also have, in contrast to all other stages, two characteristic whitish spots visible both on the carapace and on the sternum. These spots seem somewhat larger in the invasive stage than figured by Sandoz and Hopkins, who apparently failed to note them on the dorsal side. However, in proportion to the size of the crab they are much smaller in the invasive stage than in the hard stage. These spots mark the ends of two solid, cylindrical rods connecting the dorsal and ventral side of the body. They consist of a very hard, opaque substance and serve as attachments for many muscles, which probably to a large extent are the heavy musculature needed for the quick swimming movements of the third and fourth pairs of pereopods. When swimming, only

these pereopods are used while the other pairs, especially the fifth, are kept more or less motionless. Although not as soft-shelled as the pre-hard stages, the invasive stage is not nearly as firm as the hard stage.

We found that the males leave their hosts in the hard stage and proceed to enter other oysters for copulatory purposes, and indications are that the female also may change host under certain circumstances. It is, therefore, not to be wondered that the invasive stage has so many structural similarities common with the hard stage and differing from all other stages. They are all adaptive modifications instrumental for a free-living existence as well as for the invasion of the host.

Pre-hard stages

These are the hitherto undescribed instars between the invasive stage and the hard stage.

Morphologically these stages resemble post-hard crabs. Like these they have a rounded, soft-shelled carapace which yields to the touch. The pereopods are slender and without swimming hairs. More especially they resemble the second stage described by Stauber (1945). In fact we cannot distinguish with certainty between the last pre-hard and the second stage crab. Although this reflects the morphological adaptation of these stages for life within the oyster, it is still remarkable considering that the very distinctive hard stage separates them in the developmental cycle. As the male seldom, if ever, develops beyond the hard stage, this problem of stage identification applies, however, mainly to the female. It is hoped that future comparative studies of a large number of young females may make a true distinction possible.

As the smallest hard-stage crab, a female, found in our large collection measured 1.3 mm., it seems fairly certain that all soft-shelled crabs smaller than this must be pre-hard crabs. The smallest specimen found measured about 0.75 mm., and several moults, probably at least four, occur with increase in body size and development of the pleopods before the crab moults into the hard stage.

The sexes are indistinguishable except for differences in genital openings and morphology and number of pleopods. By a careful microscopical examination of the latter it was possible to determine the sex of all crabs down to a size of about 0.9 mm. This meant that practically all but the first of the pre-hard stages could be sexed with certainty.

Stauber (1945) showed that hard-stage males were larger on the average than hard-stage females, and this is also true for pre-hard crabs. Admittedly the maximum size, and therefore also the mean, of pre-hard females cannot be stated as long as the last of these stages can be confused with the second stage. Nevertheless, it is bound to be considerably smaller in the female than in the male since the largest hard stage female found measured only 2.7 mm. as against 4.6 mm. for the largest hard-stage male.

The largest soft-shelled male measured 4.2 mm., but Stauber reported one measuring 4.8 mm. With some reservation he referred males of this type to a second stage following the hard stage as he pointed out that they could also be abnormal crabs. This could be due to some sort of parasitism as reported for *P. pisum* by Mercier and Poisson (1929). When these authors found two soft-shelled males they naturally regarded them as abnormal because they differed from the (hard

stage) males normally found, and finding that these crabs were infested by the parasitic isopod, *Pinnotherion vermiforme*, they concluded that here was the cause of it. Furthermore, since the two mentioned males as well as an infested, normal male were larger than the uninfested males in their material, they also concluded that the parasite causes an increase in the size of the host. Later, however, Atkins (1933) thoroughly studied the same parasite and found that none of the 8 soft-shelled males in her material were parasitized, but, since such males were scarce, Atkins still regards them as being abnormal. She points out that the parasitized males found by Mercier and Poisson were not larger than many normal (hard stage) crabs. In view of our findings, it is obvious to conclude that these soft-shelled males are normal pre-hard crabs, but, for certain reasons given in the discussion, the possibility that a hard-stage male now and then moults into a soft-shelled crab cannot be omitted. The maximum size of pre-hard males given in Table II may therefore be too high. It should be noted, however, that Stauber's finding of a larger mean size for his soft-shelled than for his hard-stage males is probably due to a sampling error. His material included only 13 of the former specimens, and they were collected over a long period of time.

A few atypical crabs occurred in our samples which combined features from pre-hard and hard stage morphology. Some also had all the characteristics of the pre-hard stages except that the carapace did not yield to the touch. It was brittle, however, and cracked at the slightest use of force. It is hoped to return to the significance of these "abnormalities" in a second paper.

Hard stage

This is the stage described by Stauber (1945) as the invasive stage (Stage I). Many of its characteristics have already been given in the section on the true invasive stage, and there is little to add to Stauber's excellent description.

One point is of particular interest, *viz.* the two cylindrical rods connecting the dorsal and ventral sides of the body. The diameter of these structures is the same as that of the spots on the sternum, while the dorsal spots, as noted by Stauber, usually are somewhat larger and more oval in shape. In proportion to the size of the crab the diameter of a single rod is equivalent to between $\frac{1}{4}$ and $\frac{1}{5}$ of the width of the carapace. Thus the rods account for a considerable part of the endophragmal skeleton. The rods are firmly embedded in the sternum but disconnect rather easily from the carapace.

The hard stage differs markedly from the equivalent stage of *P. pisum*, specimens of which we have had the opportunity to examine. The latter have an arched carapace, possess no spots or rods, and are equipped with long, plumose swimming hairs on all walking legs. Also in contrast to *P. ostreum* the fourth and fifth pairs of pereopods appear to be the main appendages used in swimming (Darbishire, 1900).

Female hard-stage crabs ranged in size from 1.3 to 2.7 mm., thus slightly extending the range of 1.4 to 2.4 mm. found by Stauber. However, two abnormal females were found which measured 4.1 and 4.6 mm. They had evidently been retarded in development for one reason or another since one had precocious gonadal development with abnormal, gnarled pleopods, and the other had hairy, biramous pleopods which normally do not occur before the crab has moulted into the third stage.

The smallest hard-stage male measured 1.5 mm. or the same minimum as found by Stauber. The upper size range, however, was considerably extended. The largest specimen found by Stauber measured 3.4 mm. while we found many exceeding that size, the largest measuring 4.1 mm. Furthermore, the Bivalve Laboratory possesses a male collected by Mr. Franklin Flower in Delaware Bay on December 18, 1952 which we found to measure 4.6 mm. The fact that Stauber found a soft-shelled male measuring 4.8 mm. seemingly indicates that even larger hard-stage males may occur. As discussed earlier, however, such large soft-shelled males may be abnormal.

It was found that crabs which had reached the hard stage in their first fall, that is, less than two months after invasion of the host, were somewhat smaller on the average than those which had over-wintered in a pre-hard stage and did not develop into the hard stage before growth and development had commenced again the following spring.

Post-hard stages

These are the soft-shelled female growth stages described by Stauber (1945) as the second, third, fourth, and fifth stages, the latter being the mature crab.

They have a thin, membranaceous and rounded carapace which yields to the touch. The slender pereopods are subcylindrical and possess no swimming hairs. The four stages are primarily differentiated from one another on the basis of the stage of development of the pleopods and the proportional width of the abdomen (Table II).

Stauber's second stage is not clearly defined as his material included a number of pre-hard crabs. Thus he mentions (p. 282) a specimen measuring only 0.9 mm. which could not possibly have been a second stage crab. This mistake was due to the firmly established belief that the hard stage was the invasive stage. Stauber's figures of the second stage, however, agree well with the morphology of the second stage crabs reared by us from the hard stage in the laboratory.

Judging by our data it seems certain that the minimum size of the second stage cannot be less than 1.3 mm. The maximum size, as well as the size ranges of the following growth stages in our collections, agrees fairly well with the figures given by Stauber, except for the fifth stage. Here we found a size range of 4.4 to 15.1 mm. as compared to Stauber's figures of 6.0 to 14.9 mm. All size ranges are given in Table II.

As also pointed out by Stauber, morphological variations occur, a fact which now and then makes it difficult to place a given crab in a certain growth stage.

INVASION OF THE OYSTER AND SURVIVAL OF THE EARLY STAGES

As anticipated by Stauber (1945), invasion of the oyster in Delaware Bay takes place during late summer and early fall. In 1955 the first invasive stage crabs were noted on August 17th, but no oysters had been examined especially for the presence of *Pinnotheres* prior to that date. However, a careful check made through the spring and summer of 1956 again revealed no invasive stage crabs before the middle of August, *viz.* on August 16th. Nevertheless, scattered invasions no doubt occurred earlier as 1st stage zoeae were present in plankton samples on July 2nd,

TABLE II

Post-planktonic developmental cycle of Pinnotheres ostreum, based on the combined data of Stauber (1945) and the present authors

Stage of development	Range in carapace width in mm.	Most important external morphological characteristics	Biological factors
Invasive stage (First crab stage)	0.59-0.73	Flattened carapace and pereopods. Posterior margins of pereopods thickened, 3rd and 4th pairs have plumose swimming hairs. Two small, white spots on carapace and on sternum. Carapace hard around these spots.	Free-swimming until invasion of host. After invasion it is found in all parts of water-conducting system of the host.
Pre-hard stages	Male 0.75*-4.8 Female 0.75*-2.7*	Rounded carapace. Thin, flexible exoskeleton. Slender pereopods. No swimming hairs. Large females practically indistinguishable from 2nd stage crabs.	Found in all parts of the water-conducting system of the host.
Hard stage (I stage of Stauber, 1945)	Male 1.4-4.6 Female 1.3-2.7	Carapace flattened and very hard. Flattened pereopods with posterior margins thickened and with plumose swimming hairs on 3rd and 4th pair. Two large, white spots on carapace and on sternum. Males larger on the average than females.	Found free-swimming and in all parts of water-conducting system of the host. Copulatory stage. Males die in this stage.
Stage II	1.3*-3.1	Rounded carapace. Thin flexible exoskeleton. Slender pereopods. No swimming hairs. Abdomen wholly contained in sternal groove. No hairs on pleopods.	Never free-swimming. Predominantly, possibly always, found only on the gills of the host.
Stage III	2.6-4.4	Edges of abdomen extend beyond depression in sternum. First two pairs of pleopods clearly segmented and supplied with a few hairs.	Only found on the gills of the host.
Stage IV	3.6-8.9	Relative width of abdomen larger than in preceding stage, just reaching coxae of pereopods in most cases. Pleopods almost fully developed and well supplied with hairs.	As in 3rd stage.
Stage V (Mature female)	4.4-15.1	Abdominal edges covers coxae of pereopods. Pleopods fully developed. The orange gonads may be seen through the thin carapace.	As in 3rd stage.

* Approximate measurements.

and the laboratory studies by Sandoz and Hopkins (1947), as well as our field data, show that only about 25 days or less are required from hatching to the development of the first crab stage, now known also to be the invasive stage. Invasions of oysters in Delaware Bay prior to the middle of August are, however, with little

doubt on a very limited scale, at least in years with normal environmental conditions. This is also indicated by the fact that a distinct peak period of invasions occurs in early September. On August 22nd in 1956 only 3 crabs were found in 244 spat collected at Pierces Point, while 136 crabs were found in 199 spat collected on the same ground on September 23rd. Also, of 279 crabs collected there on September 17, 1955, 244 were still in the invasive stage, which indicates that a very recent mass invasion had taken place.

Since the peak period of oyster setting in Delaware Bay generally is in July, most spat will have grown sufficiently large to harbor one or more crabs by the peak of crab invasions.

It is not clear how late in the year invasions may occur as a few invasive stage crabs were found in oysters during all of the winter months. However, since growth and development stops about November 1st (Fig. 1), these crabs were probably late invaders retarded in their development by winter conditions. In 1956 a few ovigers³ were collected as late as the middle of October. And in 1942, Stauber (1945) collected an ovigerous female as late as October 19th. The embryos were then almost ready to hatch and the first zoeae were liberated 4 days later. Whether the zoeae are able to carry through metamorphosis to the first crab stage that late in the year is perhaps doubtful. The bottom water temperature of Delaware Bay generally falls to about 15° C. by November 1st and to about 5° C. by December 1st, and as it appears that the young immature crabs do not grow and develop at temperatures below the first mentioned level (Fig. 1), the larvae probably do not either.

Surprisingly small spat may be invaded. Thus infested spat of less than 10 mm. in length were often found, and in one case a spat measuring only 4.2 mm. contained two crabs. Up to 7 invasive stage crabs were found in a single spat.

Stauber (1945) observed hard-stage crabs attached to the margin of oysters with their posterior ends towards the bill. This same orientation was also noted for the invasive stage in our laboratory experiments. As free-living crabs are also known to enter enclosures backwards, *Pinnotheres* probably enters its host with the posterior end first.

Once the crab has successfully invaded its host it may be found anywhere in the water conducting system of the oyster where it may stay while developing through to the hard stage, while later stages are found only on the gills. Next to these, the promyal and suprabranchial chambers are the areas usually inhabited by crabs of the early stages.

A preference to invade spat and, secondarily, yearlings rather than older oysters seems apparent from several types of observations. On August 23, 1956 only a single 1956 crab was found in 684 yearling oysters collected in the Cohansey River Cove while the few spat present were all infested, a couple of them with more than one crab. The only extensive comparative data, however, are from the Bay Shore Channel Bed where there was a heavy set of both oysters and crabs in 1956 as there had been in 1955. Two collections, each consisting of three different age groups of oysters were taken (Table III). One was taken on September 12th during the peak invasive period and the other was taken on October 9th. The oysters were all collected in the same dredge hauls, and nearly all the spat were taken directly from yearlings and older oysters.

³ Oviger = ovigerous female. Term adopted from Ryan (1956).

As seen in Table III, only 21.5% of the older oysters were infested with 1956 crabs on September 12th, while 54.6% of the yearlings and no less than 76.7% of the spat were infested with crabs of that year class. On October 9th the differences were not so striking, a fact to which we return later.

A good number of the yearlings and older oysters were already infested with mature crabs when the 1956 set of crabs occurred (Table III, column 4). This could possibly have been one of the reasons for the preference indicated to invade spat, since the latter for obvious reasons were not already infested. Oysters with and without mature crabs were, however, invaded by 1956 crabs to about the same extent.

Possibly the preference to invade spat is more apparent than real. Failure of hard-stage crabs to invade older oysters was in some cases noted by Stauber (1945), indicating that the invasion is not always easily accomplished. Even if it is, the yearlings and especially the older, larger oysters may possibly still be able to cope with a good number of the tiny invasive stage crabs by enveloping them in mucus and pass them out by ciliary action and clamping of the valves.

TABLE III

Comparison of infestations with P. ostreum in three different age groups of oysters on the Bay Shore Channel Bed during and after the main invasive period

Date of collection	Age group of oyster	Number of oysters examined	Per cent infested with 1955 or older crabs	Per cent infested with 1956 crabs	Per cent of 1956 crabs in hard or post-hard stages	Per cent oyster with two or more 1956 crabs
Sept. 12th, 1956	Spat	167	0.0	76.6	3.1*	31.1
	Yearlings	339	33.6	54.6	47.3*	15.3
	Older oysters	186	50.0	21.5	90.0*	4.3
Oct. 9th, 1956	Spat	180	0.0	77.2	20.9	7.8
	Yearlings	289	34.4	72.7	73.9	27.3
	Older oysters	117	51.3	52.1	82.6	15.4

* An asterisk indicates that only hard stage crabs were found.

Mytilus edulis has been observed to expel inserted megalopa of *P. pinnotheres* by Atkins (1955).

A comparison of the data in Table III, column 5, reveals that the incidence of oysters infested with 1956 crabs rose considerably for the yearlings and older oysters between the two sampling dates while it remained practically constant for the spat. In fact, the absolute number of crabs decreased in the latter group while it increased even more in the other two age groups than the data in column 5 indicate. This is seen in column 7, which shows that the incidence of multiple infestations with 1956 crabs decreased sharply in the spat from 31.1 to 7.8% but increased in the yearlings from 15.3 to 27.3%, and in the older oysters from 4.3 to 15.4%. Considering that the crabs apparently prefer to invade spat these data seem somewhat contradictory. An analysis of these and other data indicates, however, that the apparent paradox can be explained as being due to a higher mortality rate in crabs invading spat than in those invading yearlings and older oysters.

As stated above, only the absolute number of crabs found in spat decreased while the percentage of spat infested remained constant. In other words, the decrease in number of crabs between the two sampling dates was apparently either due to the death or the migration of crabs from spat containing more than one crab. Losses among "single" crabs possibly also occurred; if so, they were made up for by intermittent new invasions of crabs. The same trend that only one crab will survive in the same spat was also noted in 1955 at Pierces Point as well as on the Bay Shore Channel Bed. Only during the peak invasive period in September could spat with 3 and up to 7 crabs be found. A few weeks later only double infestations could be found, and the incidence of their occurrence was less than 10%. By the end of February, 1956 practically no spat contained more than one crab, and even a good number of "single" crabs apparently died during that month (Table I, Fig. 5). These mortalities came after a prolonged period of very low temperatures (Fig. 1), thus indicating that even "single" crabs are easily endangered by adverse environmental conditions.

The increase in number of yearlings and older oysters containing more than one 1956 crab between the two sampling dates (Table III) indicates in itself that the crabs survive better in these oysters than in spat. Further evidence of this is given in the same table (column 6). For both dates it is seen that a much lower percentage of the 1956 crabs had reached the hard and post-hard stages in spat than in the other oysters. This fact, together with the data given on crab-host size relationship in a later section, clearly shows that the crabs grow and develop considerably slower in spat than in larger oysters. In other words, the crabs thrive better in yearlings and older oysters, and it is therefore not surprising that they also survive better. The reasons for this will be discussed later. It is stressed, however, that a quicker rate of growth and development is probably in itself of prime importance for the survival of the crab during its first fall and winter since it is very likely that the earliest stages cannot withstand adverse conditions as well as later stages.

In summing up the data in Table III it may be concluded that intermittent invasions of crabs between the two dates, and a higher mortality rate of crabs invading spat than of those invading other age groups of oysters, constitute the main reasons why the yearlings and older oysters in direct contrast to the spat showed an increase in incidence of infestation on October 9th.

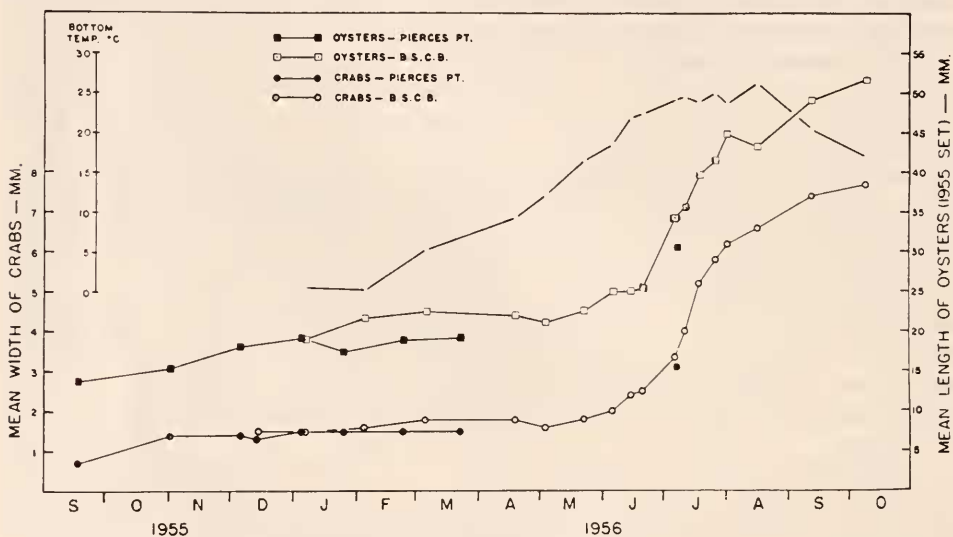
It was also considered whether the data in Table III could be at least partly explained by migrations of hard-stage crabs from spat to other oysters. However, since all the observed differences between the two sampling dates can be explained otherwise, while migrations could explain only little of it, the latter probably did not take place to any large extent. Furthermore, the available data indicate that the "loss" of crabs inhabiting spat occurred at a time when only few of these crabs had developed into the hard stage, *i.e.*, before these crabs were capable of migrating.

GROWTH AND DEVELOPMENT

Unless otherwise stated the following statements and discussion of results are based on studies of populations of *Pinnotheres* growing and developing in spat. This point should be kept in mind, because, with other factors being equal, growth and development would differ, depending on the size and age composition of the host population of oysters.

Growth curves, as represented by the mean sizes of all the crabs and their host oysters for each sampling date at Pierces Point and the Bay Shore Channel Bed, are plotted in Figure 1, together with a curve showing bottom temperatures at the latter station. The numbers of oysters and crabs on which the data plotted are based are listed in Table I. Both grounds were not sampled through the entire collecting period from September 17, 1955 to October 9, 1956, but there was a considerable period of overlapping between the beginning of sampling on the Bay Shore Channel Bed and the termination of sampling at Pierces Point.

On the first collecting date in September, 1955, 87.5% of the crabs found were still in the invasive stage, thus indicating that the spat had become infested very recently. On the other hand, since the incidence of infestation was higher than on any subsequent sampling date at Pierces Point it may also be concluded that the peak invasive period had terminated.



were post-hard crabs, no less than 62.7% of them having already reached the final stage. By August 16th, 95.5% of the collected females were mature, more than half of them being ovigers. Thus, as suspected by Stauber (1945), *P. ostreum* reaches maturity in Delaware Bay within its first year.

The remarkable correlation between the growth curves of the crab and host populations in Figure 1 should be noted, although it is not so surprising considering that the crab is dependent on the food gathered by its host.

Males live only one year or less. One of the curves in Figure 5 shows the percentage of crabs in the hard stage, and another shows the sex ratio (as % females) for each collecting date on the Bay Shore Channel Bed. It will be seen that the majority of the crabs developed into the hard (copulatory) stage within a limited period of time around June 20th whereupon the males began to disappear from the oysters. Until and including that date, about 45% of the crabs were males but by July 26th, the percentage was only 6.7, and by September 12th no 1955 males could be found. It is shown in a later section that the males left their hosts in search of females in other oysters, and there is every indication that they did not commence a longer free-living life but died shortly after copulation with one or more females. All the above facts also constitute an important part of the evidence which shows that the males normally do not develop beyond the hard stage, *i.e.*, that no true second stage male exists.

The females continue to grow after they have hatched their first batch of eggs during the summer. The mean size of the 1955 crabs, all mature females, collected from yearlings on October 9, 1956 was 7.68 mm. with a size range of 5.2 to 10.0 mm. And this mean, as well as the maximum size, was the highest recorded for any sample taken from yearlings in 1956, no further samples having been taken after that date (Table I). Since we know that a positive crab-host size relationship exists, these figures do not necessarily apply to crabs invading oysters other than spat. However, the mean size of fourth stage crabs taken from older oysters was less than 6 mm., and we never found one as large as 8.9 mm. as Stauber (1945) did. This indicates that only few females will reach a size exceeding 10 mm. in their first year even in older oysters. And it seems almost certain that none will attain this size before growth is renewed after hatching of the eggs. How soon this growth commences is not known, but Freame (1943) observed an ovigerous *Pinnotheres* sp. moulting 10 days after hatching of the last eggs in the laboratory. Since very few one-year-old ovigers occur before the middle of July and since the egg-bearing period is 3 to 5 weeks, it is clear that all females collected in spring and early summer which had a size exceeding 10 mm. must have been crabs in their second (or third) year. The latter possibility is indicated by the fact that very large crabs may be found in older oysters just prior to, but before, growth begins in the spring. Berner (1952) also found that female *P. pisum* kept in aquaria became 3 years old.

Some indication of the rate of growth after the first year may be had from the data presented in Figure 2. It shows the size distribution of all ovigers found in two age groups of oysters, *viz.* yearlings (1955 spat) and older oysters, from collections made in August, 1956 on the Bay Shore Channel Bed. Judging by the difference in mean size of the two groups of crabs, an average increase in carapace width of about 3.5 mm. after the first year of growth is indicated. However, while the crabs collected from yearlings represented a true one-year age group, a number

of the ovigers found in the older oysters were no doubt also only one year old, as judged by their relative small size and the fact that 16 immature crabs were also found in these oysters. This factor is no doubt the cause of some of the overlapping in size distribution of the two groups of crabs. The actual mean increase therefore probably amounts to at least 4.0 mm. Most of this growth probably takes place before the crab is two years old.

As stated earlier, a few of the crabs invading the 1955 spat developed as far as the third stage before growth was terminated by winter conditions. In the fall of 1956 this was the case to a much larger extent with 1956 crabs invading spat of that year class. Of 158 crabs collected from spat on the Bay Shore Channel Bed on October 9th, 26 had developed beyond the hard stage, one of them having reached the fourth stage. Forty-five of the crabs were too small to be sexed, but

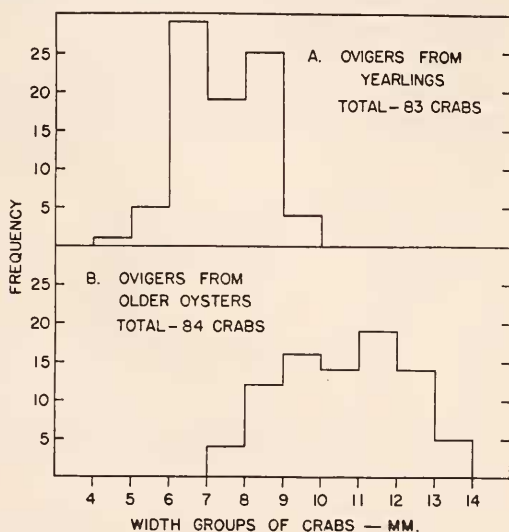


FIGURE 2. Size distribution of (A) ovigers collected from yearling oysters, and (B) ovigers collected from older oysters. Both groups of oysters were collected on August 1st and 16th in 1956 on the Bay Shore Channel Bed.

of the remaining, only 38 were males as opposed to 75 females. This indicates that the 26 post-hard crabs represented about 25% of all the females present. In contrast, only nine post-hard crabs were found among 205 crabs collected from spat on the same ground as late as December 14th in 1955. Indications are that the spat grew faster in the fall of 1956 than in the preceding year. This may well account for the observed differences, considering that the growth (and development) of a *Pinnotherea* population is correlated with the growth of the host population (Fig. 1). The latter fact will be demonstrated on an individual basis in the next section.

GROWTH AND DEVELOPMENT IN RELATION TO SIZE OF HOST

Atkins (1926) found a rough size relationship between 34 *P. pisum* and their host mussels in spite of the fact that the author was dealing with different age

groups of both crabs and mussels. The latter was also true for the material used by Wells (1940) who, nevertheless, could demonstrate a clear size relationship between *Fabia subquadrata*, of the same sub-family as *Pinnotheres*, and its host *Modiolus modiolus*.

The following information is all based on data from collections of 1955 crabs from 1955 spat, which were taken in 1956 before the 1956 year class of crabs appeared, thus insuring that we were dealing with a known year class of both crabs and oysters.

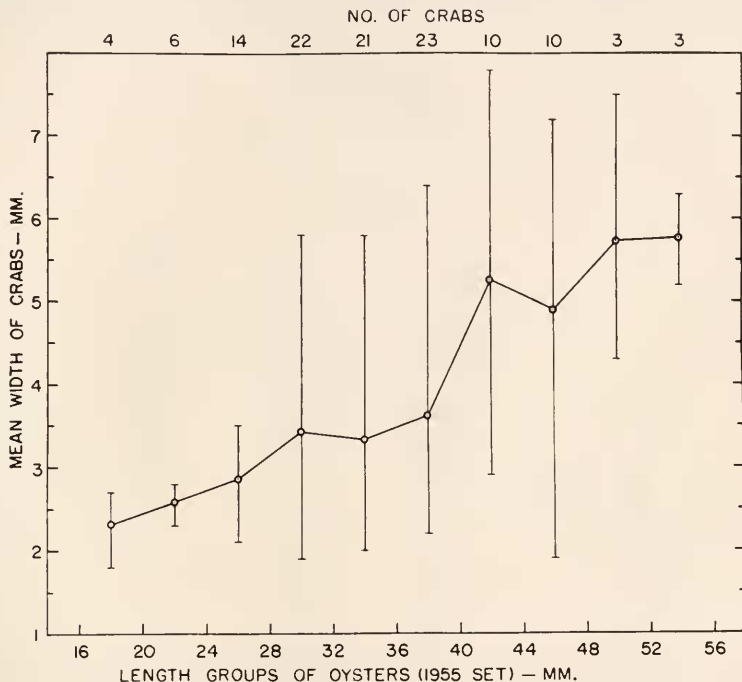


FIGURE 3. Crab-oyster size relationship. The mean width and size range is shown for all crabs, irrespective of stage, found in each 4-mm. length group of yearling oysters collected on the Bay Shore Channel Bed on July 6, 1956. All these crabs were for obvious reasons of the 1955 year-class.

In Figure 3, the mean sizes and size ranges of all crabs, irrespective of stage, found in each 4-mm. size group of oysters have been plotted for a collection made on the Bay Shore Channel Bed on July 6, 1956. A definite positive correlation between crab and oyster size is clearly present.

Plottings of the same kind, as well as statistical analysis, were undertaken for several other regular samples and they all show the same size relationship. It is not absolute, insofar as small crabs may well be found in large oysters, but the opposite is not the case. In other words, the factor or factors which limit the growth of the individual host also directly or indirectly limit the growth of the crab. Probably the most important factor is the amount of available food, which largely depends on the environmental conditions surrounding the individual host oyster.

While *growth* of the crab is retarded in slow-growing spat, there is evidence to show that *development* is not affected to a comparable extent. It may be safely assumed that having moulted into the fifth stage the females do not moult again before they have hatched their first batch of eggs. This means that any sample of mature females collected from yearlings before September will contain only an insignificant number of crabs which have grown since moulting into the fifth stage. In spite of being in the same stage of development, crabs from such samples vary, however, in size to an extraordinary degree. This, among other facts, is illustrated in Figure 4, which is based on the largest sample of young fifth stage crabs

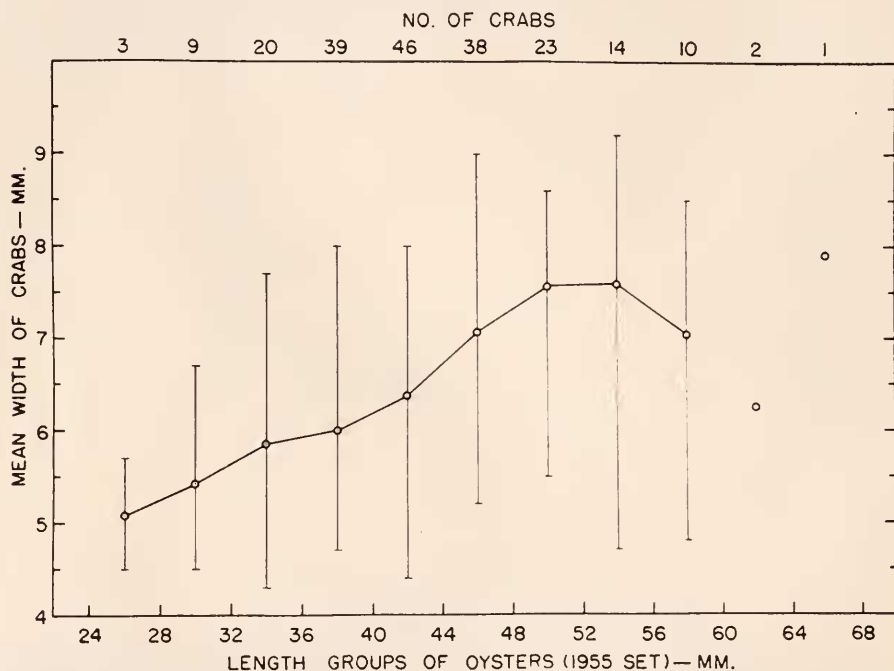


FIGURE 4. Size relationship between crabs in the same stage of development and their host oysters. The data, which are plotted as in Figure 3, are based on all fifth stage crabs collected from yearling oysters in the Cohansey River Cove on August 23, 1956. These oysters had been transplanted from the Bay Shore Channel Bed in early July.

taken on a single date. The data presented reveal the same positive crab-host size (and growth) relationship as was demonstrated above on the basis of samples containing crabs of nearly all developmental stages. It appears, therefore, that the females simply develop into the fifth stage at a smaller size in smaller, slow-growing oysters than they do in larger, faster growing specimens. A further example of this is given in Figure 2. As discussed earlier, some of the smaller ovigers collected from the older oysters were no doubt only one year old. Yet none of them measured less than 7 mm. while the one-year-old ovigers taken from the yearlings comprised many specimens smaller than this. It should be stressed, however, that our data only point to the conclusion that the growth of the crab

is more affected by environmental conditions than is the development. Naturally the time element involved in the latter will also be affected under adverse conditions such as an insufficient food supply. A good example of this is given by the difference in rate of development of the young crabs in 1955 and 1956 which was mentioned in the preceding section.

GROWTH AND DEVELOPMENT IN RELATION TO MOULTING

Information on the size increase after moulting of individual crabs was obtained in two ways. In some cases the old exoskeleton was still present, together with the moulted crab, in oysters brought into the laboratory. In other cases,

TABLE IV
Moulting in Pinnotheres ostreum

Date of moulting	Sex of crab	Carapace width in mm. and stage of crab		Increase in carapace width in mm.	Increase in % of original carapace width
		Before moulting	After moulting		
17- 9-55	?	0.66 I.S.	0.76 P-H.	0.10	15.0
22- 8-56	?	? P-H.	0.95 P-H.	—	—
10- 9-56	M.	2.90 P-H.	2.90 P-H.	0.00	0.0
20- 8-56	M.	4.10 P-H.	4.00 P-H.	-0.10	—
3- 9-56	M.**	3.30 P-H.	3.30 H.	0.00	0.0
8-10-56	F.	1.70 H.	1.95 II.	0.25	14.5
16- 7-56	F.**	1.80 H.	1.80 II.	0.00	0.0
4-10-56	F.	1.85 H.	2.15 II.	0.30	16.0
8-10-56	F.	1.90 H.	2.25 II.	0.35	18.5
6- 7-56	F.*	2.05 H.	2.40 II.	0.35	17.0
27- 7-56	F.*	5.40 IV.	6.10 IV.	0.70	13.0
30- 7-56	F.*	5.40 IV.	5.90 V.	0.50	9.0
?- 7-56	F.*	5.50 IV.	7.00 V.	1.50	27.5
9-10-56	F.*	9.90 V.	11.50 V.	1.60	16.0
9-10-56	F.*	11.90 V.	11.90 V.	0.00	0.0
6-10-56	F.	12.80 V.	13.30 V.	0.50	4.0

Symbols: I.S. = Invasive stage. P-H. = Pre-hard stage. H. = Hard stage. II., IV. & V. = 2nd, 4th & 5th post-hard stages.

Crabs marked with one asterisk moulted in nature.

Crabs marked with two asterisks had not hardened properly after moulting when the measurements were taken.

moulting occurred in the laboratory from crabs of known stage, sex and size placed in oysters by the method previously described.

The laboratory experiments were performed primarily to secure: 1. Moulting of large soft-shelled males (into the hard stage) to test field information that these are pre-hard stage crabs. 2. Eventual moulting of hard stage males as a control for (1). 3. Moulting of hard stage females to secure known second stage crabs. As was expected, moultings of types (1) and (3) occurred while all hard-stage males died after some time.

All available data are given in Table IV, in which it may be noted that in some

cases there was no apparent increase in carapace width after a moulting had occurred. This is probably due to the fact that some recently moulted crabs were preserved too soon after moulting and consequently the body had not had time to assume its normal shape. The poor food supply in the aquaria was no doubt also partially responsible for no size increase. If these moultings are disregarded, the data indicate a mean increase in carapace width of about 15% after each moult, regardless of the previous size and stage of the crab. If this be true, it would take about five moults for the invasive stage crab to develop through the pre-hard stages into the hard stage. Preliminary morphometric studies of pleopod length and development in relation to body size of our collection of pre-hard stage males seem to verify this. Supporting evidence is the fact that a pre-hard stage crab measured only 0.95 mm. after it had moulted from another pre-hard stage which was no doubt the stage immediately following the invasive stage. Since pre-hard and hard-stage males are larger on the average than females of the equivalent stages, differences may exist in the average number of moults and size increase in the two sexes. More detailed studies are necessary to check on these points.

Only one of the nine fairly large pre-hard males used in our experiments moulted into the hard stage, while two others moulted without a change of stage. Although the former was only slightly larger than the mean size of Stauber's 13 "2nd stage" males, the moulting still serves as a support of other evidence previously referred to, that no true second stage exists in the male. More important is perhaps the fact that all hard stage males brought into the laboratory died within a few weeks while hard and post-hard stage females could be kept alive for many weeks, even in the less favorable environment of the Petri dishes, and with a very poor food supply. Moulting experiments were done with seven hard stage males, none of which moulted, nor did other hard stage males in Petri dishes. In contrast to this, four out of six hard stage females inserted into oysters moulted into the second stage (Table IV), indicating that there was no reason to suspect that hard-stage crabs for one reason or another were unable to moult under laboratory conditions. Nor is further development of the hard stage dependent on copulation as suggested by Orton (1921) and Atkins (1926) for *Pinnotheres pisum* (see next section).

Moultings of fifth stage crabs were noted several times by Stauber (1945) as well as by the present authors. In view of the mean increase in carapace width of about 4 mm. or more which takes place after the crab has first developed into the fifth stage it seems likely that at least three moults occur in this stage before the maximum size is reached. Since the crab may develop into the fifth stage at a size anywhere from 4.4 to 8.9 mm. (Table II), depending on environmental conditions, the number of these moults must, however, vary to some extent.

It seems probable that growth moultings with little or no morphological changes may occur in all stages with the exception of the invasive stage and probably also the hard stage. Such moultings probably explain why a few crabs, being intermediate in character, could not be placed with certainty in one or another of the otherwise well defined growth stages.

Since *Pinnotheres* copulates precociously it differs from most brachyurans in moulting between copulation and egg-deposition. As the female usually receives sperm while in the hard stage at least four such intermediate moultings may occur.

COPULATION, EGG-DEPOSITION, HATCHING, AND LARVAL LIFE

Thompson (1835) assumed that the male of *Pinnotheres pisum* goes from host to host in search of females during the copulatory period. This was verified by Orton (1921) who found males trapped between the valves of the host, *Mytilus edulis*. He also found a hard stage female with its spermathecae filled with mature sperm, thus showing that this crab copulates at an extremely early age. Sperm was also found in the spermathecae of later stages, including the fifth stage. Atkins (1926) corroborated Orton's findings, but she also found a few fifth stages without sperm, and this led her to state that a second copulation possibly took place. Stauber (1945) doubted that this could be the case in *P. ostreum* because it would involve copulation between crabs which in his opinion differ too much in size. It may here be mentioned that the male of *P. pisum* is considerably larger on the average in relation to the size of the female than is the male of *P. ostreum*. Berner's (1952) paper, which contains many statements on the biology of *P. pisum*, unfortunately lacks vital information on materials and methods, and the author has taken no notice of later papers on the subject than that of Orton (1921). He states that the free-swimming male seeks mussels containing females which are about one year old, and that after copulation, the male again leaves the host as the ovigers are always found alone. The author refers to Orton's finding of precocious copulation, but also states that copulations involving mature females took place in his laboratory tanks. It appears, however, that this statement is based solely on the author having seen males close to females, and the occurrence of egg-deposition by females long after they had been collected. A number of other papers contain valuable contributions on the reproductive biology of pinnotherid crabs, but they are best dealt with in connection with our own observations.

In the present studies an attempt was made to gain information on the reproductive activities of a known year-class of crabs from a single locality, thereby eliminating as many variable factors as possible. Delaware Bay proved to be particularly well suited for this purpose since the extreme variations in water temperature between the seasons of the year give rise to distinct, short peak periods of the different phases involved.

Most of the information gained is illustrated in Figure 5. The data plotted are based on the material from regular samples taken on the Bay Shore Channel Bed, consisting of 1955 crabs from 1955 spat (Table I), and an extra sample (see figure legend).

One of the curves (Hard crabs) shows that the percentage of hard-stage crabs remained at a consistently low level throughout the winter and spring, *viz.* during the period in which it was shown earlier (Fig. 1) that no growth took place. In June, however, the large majority of the crabs developed into the hard stage almost simultaneously. A distinct maximum occurred around June 20th, when about 66% of all the crabs collected were hard-stage crabs. Many of them had a soft carapace, indicating a very recent moulting into the hard stage.

Another curve (Female crabs) shows that on the same date there were still as many males present as in all earlier samples, *viz.* about 45% of all crabs collected. After June 20th, however, they began to disappear rapidly, as evidenced by the rising percentage of females in each subsequent sample. Towards the end

of July, less than 5% of the collected crabs were males, and by early September not a single 1955 male could be found.

Also beginning on about June 20th, the incidence of infestation (Oysters infested), which had remained at a constant level, around 58%, since February, began to fall quickly. It continued to do so until the number of males occurring in the samples became insignificant. Then the incidence again became constant, but now at the lower level of about 35%, or just about the level where it would have been on June 20th if only the females had been considered.

A fourth curve (Double infestations) in Figure 5 shows that within the same period of time, beginning towards the end of June, a notable number of double infestations began to occur. Those shown for the winter months were due to

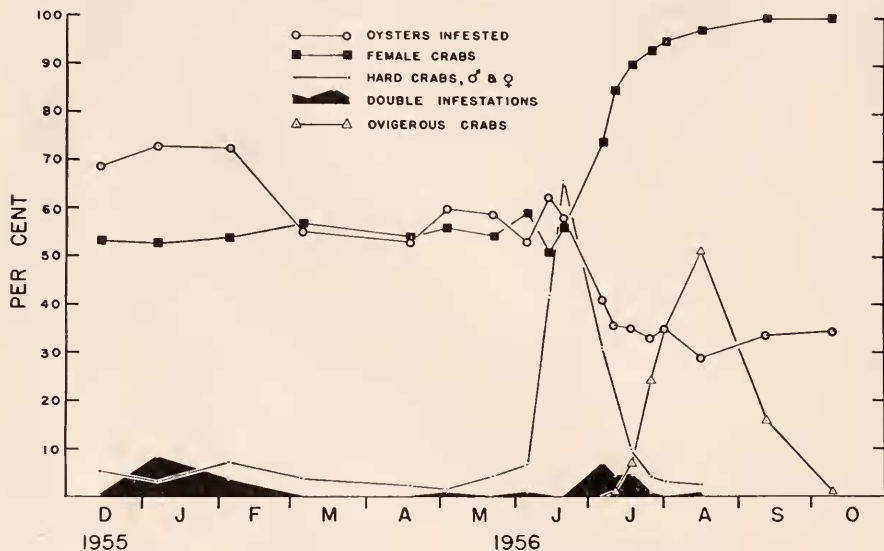


FIGURE 5. The curves show: 1. Incidence of infestation and double infestations of the 1955 year-class of oysters on the Bay Shore Channel Bed, and 2. Sex ratio (as per cent females) and development (in part) of the 1955 year-class of *P. ostreum* inhabiting these oysters, in the period from December 14, 1955 to October 9, 1956. Data on double infestations include results obtained from extra sample of 334 infested spat collected on July 11th, 16 of which were double infested.

original multi-infestations by invasive stage crabs, but those which occurred during the summer could only be due to new invasions by hard stage crabs. An examination of this summer material showed that each double infestation consisted of one crab of each sex. Such pairs were also found in collections made on other grounds during this period of the year. In a few cases two or three males had invaded the same oyster containing a female. It was significant that the males and females making up these pairs nearly always were found close together on the gills of the host while the crabs found together in the same host during the fall and winter nearly always were found widely apart from one another.

All these facts, illustrated in Figure 5, can be interpreted only in one way, *viz.* that having developed into the hard stage, the males left their host to search for

females in other oysters. Having copulated with one or more females they probably died within a few weeks or less. The latter statement is based also on the fact that a few of the males found together with females were already dead.

Even before the males began to disappear we generally found somewhat fewer males than females. For this reason, and because a number of males may be devoured by predators during their temporary free-swimming existence, it seems reasonable to deduct that a male will copulate with more than one female. At least there is every indication that all females become ovigerous in their first summer, and this could hardly be accounted for otherwise.

Of 33 pairs found in yearlings from the Bay Shore Channel Bed in July, 1956, 32 of the males were in the hard stage, while 21 of the females were either in the hard or the second stage. The remaining females were all in later stages of development, a few having reached the fifth stage. This does not necessarily mean, however, that males can or do copulate with post-hard females. Possibly they may live up to a few weeks after copulation, staying in the last oyster they visit, while the female continues development into later stages. The great rapidity of growth and development of the females in late June and in July (Fig. 1), and the fact mentioned earlier that some of the males found together with females were dead when collected, would support such a conclusion. The few of the hard and second stage females from double infestations which we examined had sperm in their spermathecae, a fact which also serves as circumstantial evidence leading to the conclusion that the females were probably all fertilized while in the hard stage.

Nevertheless, the above evidence is not conclusive, especially since other observations indicate that males may copulate with later stages. Of six known second stage crabs of the 1956 year-class examined in the fall of that year, only one contained sperm. Theoretically such females could of course remain unfertilized or become capable of producing infertile eggs only, but this does not seem a likely explanation. In the laboratory we also once observed a hard stage male, with its pleopods extended, enclosed under the abdomen of a fifth stage female. However, whether an actual copulation took place or not, we do not know. Berner's (1952) statement that female *P. pisum* may be fertilized in the fifth stage is not based on conclusive facts, which does not mean that it could not be true. The author did not observe an actual copulation, and the crabs which became ovigerous in the laboratory tanks may well have had sperm in their spermathecae when they were collected (see below). More information is certainly needed to settle the question.

The observations referred to above enlighten, however, our understanding of another point of interest. Orton (1921), and also Atkins (1926) suggested that further development of the hard stage female of *P. pisum* depended on copulation. Since known second stage crabs containing no sperm were found, this cannot be true for *P. ostreum*, and there is little reason to suspect that different species of the same genus should differ in this respect.

Atkins (1926) stated that it was extremely probable that the first implantation of sperm was sufficient to fertilize several batches of eggs in *P. pisum*. That it is sufficient for at least the first two batches was actually shown by the same author in a later paper (Atkins, 1955). She kept several female *P. pisum* isolated in the laboratory, and one of these deposited eggs on September 27, 1952 and again on May 26, 1953. Our data point to the same conclusion for *P. ostreum*. Twenty-one mature females were examined during the fall of 1956. Of these all but one

had sperm in their spermathecae, although all of them probably had been ovigerous during the preceding summer. Theoretically they could have received sperm from 1956 males, but since only one of the 1956 second stage females examined during the same period contained sperm, this seems extremely unlikely.

The fact that a fertilized 1956 female was found in the fall of that year reveals that copulation is not restricted to the early summer as the data in Figure 5 so strongly indicate.

This poses the question whether males which copulate in the fall may live through the following winter and perhaps copulate again the following early summer. In this respect it may be significant that there were fewer males than females in our regular samples from the Bay Shore Channel Bed even before the males began to disappear entirely. Sampling on that ground did not begin before December, that is, after a probable initial copulatory period was terminated by winter conditions. The "deficiency" of males may therefore have been due to a natural death of males after copulation in the fall. Some of them may also have fallen prey to predators while moving from one oyster to another in search of females. The case mentioned earlier where only 38 out of 113 sexable crabs, or 33.6%, were males points to the same conclusion. This collection was made from spat on October 9, 1956, and it will be recalled that a considerably higher percentage of crabs invading spat reached the hard stage before the onset of winter in 1956 than in 1955. There is therefore also little doubt that a higher percentage of males became sexually active in the fall of 1956 than in the preceding year. Hence, if the above hypothesis on the "missing" males is correct, one would also expect that a higher percentage of males died in the fall of 1956 than in the fall of the preceding year, and this is exactly what our data indicate. While we have good data on the 1955 year-class, this is not, however, the case for the 1956 year-class. The sex ratio of the latter group, 33.6% males, is based on the single collection from October 9th, a date which furthermore falls so early in the fall growing season, that changes may well have occurred before winter conditions stopped growth and development as well as sexual activities. Nevertheless, there can be little doubt that early summer is by far the main copulatory period for *P. ostreum* in Delaware Bay under normal environmental conditions.

While copulation may take place either in the fall or the following early summer, egg-deposition of crabs in their first year does not occur before early July. Thus, in 1956 the first oviger from a yearling (1955 spat) was taken on July 11th, and no oviger less than 10 mm. in size occurred in older oysters before July 6th. The last one-year-old ovigers were found on October 9th. The curve (Ovigerous crabs) in Figure 5 shows the percentage of 1955 crabs being ovigerous on all collecting dates on the Bay Shore Channel Bed. The highest incidence occurred in middle August when more than 50% of the collected crabs were egg-bearing females. This was also the case elsewhere in the Bay, and the following case may be mentioned. In early July of 1956 a large number of yearlings were transplanted from the Bay Shore Channel area to the Cohansey River Cove about 24 nautical miles farther up the Bay. Of 205 females collected from these oysters on August 23rd, nearly 60% were ovigers. Of these, 26% had dark brown eggs or had already begun to hatch zoeae which could be found in large numbers in the mantle cavity of oysters containing such crabs. Judging by the data illustrated in Figure 5 as well as other information, a female may copulate in the hard stage and develop into a fifth

stage oviger within a period of four to six weeks. The smallest oviger found in our collections measured only 4.5 mm.

In their second (and third) year the females may become ovigerous somewhat earlier. This is probably because they do not have to utilize a great deal of food for rapid growth and development prior to the deposition of the eggs as is the case for the one-year-old crabs. Nor do they have to await the visit of hard stage males, which do not become abundant before sometime in June, as they already have sperm in their spermathecae. In 1956 several ovigers exceeding 10 mm. in size were collected from older oysters on June 14th, or about three weeks before one-year-old ovigers were found. Judging from our data derived from a material of older crabs collected at intervals from May 22nd to October 9th in 1956, the peak period of egg-deposition also occurs two to four weeks earlier than for one-year-old crabs. From a comparison of the size distribution within these samples it also seems that, although some crabs no doubt become three years old, many of them probably die after they have hatched their eggs the second summer.

The newly deposited egg mass is orange in color. It changes gradually from a deep orange to a light brown and finally to a dark brown color. The eggs measure about 300 microns in the hatching stage (Stauber, unpublished) or about the same as in *P. pisum* (Lebour, 1928). Ovigers measuring 9.4 and 10.8 mm. in width carried 7957 and 9456 eggs, respectively. An oviger of *P. pisum* in the Copenhagen University Museum, measuring 10.4 mm., carried more than 5800 eggs. Berner's statement that this species deposits about 100 eggs is therefore erroneous.

It is not known for how long the female carries its eggs, either in Delaware Bay or elsewhere. An ovigerous *Pinnotheres taylori* brought into the laboratory on March 16th (1933) did not hatch before the first week of May (Hart, 1935). The egg-deposition and hatching of six *P. pisum* was observed in the laboratory by Atkins (1955). She found that the egg-bearing period varied between 35 and 59 days, stating that temperature differences probably constituted the main reason for the notable time difference, and that the period would no doubt be shorter in nature. Atkins also brought a *P. pinnotheres* with eggs in the early stages into the laboratory, and here hatching occurred after 40 days. Our field data from Delaware Bay, partly illustrated in Figure 5, indicate a somewhat shorter egg-bearing period for *P. ostreum*. As noted earlier, the first one-year-old oviger did not occur before July 11th, or possibly July 6th, but the peak occurrence came already in middle August. The fact that Sandoz and Hopkins obtained zoeae from a *P. ostreum* carrying a bright orange egg mass after only 12 days in the laboratory points to the same conclusion. We believe the egg-bearing period in nature to be three to five weeks. While it is almost certain that only one batch of eggs is produced in the first spawning season, the possibility that some crabs may spawn twice in the second (and third) year cannot be omitted.

As part of the oyster research program in Delaware Bay in 1956, approximately one thousand plankton samples of a hundred liters each were collected from June 14th to September 12th. This gave us an opportunity to gain some knowledge on the occurrence of *Pinnotheres* larvae. All samples from the Bay Shore Channel Bed and within a radius of about 5 nautical miles were therefore checked for the presence of such larvae.

The first zoeae were found on July 2nd and the last on August 20th, but, while samples were collected almost daily up to the latter date, rather few samples were

taken thereafter. However, four samples of a thousand liters each instead of the normal volume were taken on September 12th. In Chesapeake Bay, Sandoz and Hopkins (1947) found oyster crab larvae in the plankton from June through August, but they also took few samples outside this period. In our own samples, 137 first stage and one second stage zoeae were collected while none of the later stages, nor the megalopa, were encountered. Two invasive stage crabs were taken, however, one on August 31st and another on September 9th.

Fifty-four of the 137 first stage zoeae were found in a single bottom sample from the Maurice River Cove on July 11th. Since numerous samples contained no larvae, and since the remaining 83 specimens were collected in 35 different samples, the occurrence of so many zoeae in a single sample seems strange. It is therefore highly possible that the aperture of the sampling hose happened to pass close to an oyster containing a crab which was in the process of liberating zoeae.

Seventy of the 83 larvae mentioned above were caught between July 20th and August 20th. Although few samples were taken after the latter date, this still indicates a peak occurrence of first stage zoeae within the above period since the data correspond well with the finding of a peak occurrence of older ovigers in the latter half of July and of one-year-old ovigers in middle August, as well as with the known peak invasive period that falls in early and middle September.

Hart (1935) found that the first crab stage of *Pinnotheres taylori* emerged four weeks after hatching in the laboratory. Also in the laboratory, Sandoz and Hopkins (1947) observed the first crab stage of *P. ostreum* emerging about 25 days after hatching. No other species of pinnotherid crabs have, as far as we know, been reared to the first crab stage. Since data from the same ground (Bay Shore Channel Bed) and from the same year (1956) show (1) a distinct peak in number of ovigers in middle August, and (2) a distinct peak period of invasions in early and middle September, there is every reason to believe that the average length of larval life of the oyster crab in Delaware Bay does not exceed 25 days as found by Sandoz and Hopkins under laboratory conditions. It is probable that it is even shorter as judged from the data above and the fact that the larval development may be slowed down under laboratory conditions as pointed out by Atkins (1955). The above data and conclusions are admittedly based on one-year-old ovigers only, as older crabs deposit eggs somewhat earlier in the season. However, the former year-class constituted the large majority of the adult population in 1956, indicating that the peak invasive period was determined by invasive stage crabs deriving from the yearling crabs. Our data also indicate that the crabs invade a host as soon as they have developed into the invasive stage.

Although the first zoeal stage exhibits a distinct positive phototropism in the laboratory, only 18 of the collected specimens were taken in surface samples. This is in good accord with laboratory observations on other species of this genus. Lebour (1928) states that the newly hatched larvae of *P. pisum* at first rise to the surface but soon go to the bottom where they feed. The zoeae of *P. maculatus* seek the bottom after three to five days (Welsh, 1932), and those of *P. latissimus* do it after only one or two days (Miyake, 1935).

THE CRAB-OYSTER ASSOCIATION

Coupin (1894) discovered that *P. pisum* feeds on food filtered from the water by its host. This has been confirmed by later authors including Orton (1921)

who, through "windows" in the host's valves, observed how the pea crab picks food strings from the margins of the gills with its chelipeds. MacGinitie and MacGinitie (1949) used the same method in observing the feeding activities of *Fabia subquadrata* (referred to as *Pinnotheres concharum*). Stauber (1945) found that *P. ostreum* feeds in the same manner but that it will also catch newly formed mucus-food masses with its walking legs, then reach beneath its abdomen with its chelipeds, comb the legs, and pass the food on to the mouth.

How young crabs feed when inhabiting parts of the oyster other than the gills is not known. MacGinitie and MacGinitie (1949) observed that the pea crabs *Scleroplax* and *Pinnixa* are able to filter food from the water by their feathery mouth parts. These crabs belong to another sub-family than *Pinnotheres* and may therefore differ from the latter genus in this respect. However, several species of *Pinnotheres*, such as *P. pugettensis*, *P. taylori*, and *P. pinnotheres*, live in the excurrent region of the atrial cavity of tunicates. And they must, as pointed out by Wells (1940), take their food from the water brought in by the host to serve as a source of food for the tunicate itself. The crabs can hardly do this in any other way than by filtering the water with their mouth parts. It is therefore very likely that immature *P. ostreum* may also feed by the filtering method. Such a feeding method could explain why a large number of immature crabs in a single oyster does not seem to affect the tissues of the host more than one crab as observed by Stauber (1945). However, this manner of feeding is probably not effective enough for the older stages. Post-hard stage crabs are found only on the gills, indicating that only the feeding on the food-laden mucus strings can secure the crab enough food for the rapid growth and development and the production of eggs which take place in late spring and summer. In any case, whether the young crabs feed by one or the other method or both, it is dependent on the amount of food particles brought into the oyster per time unit. It is therefore highly possible that the difference in survival of oyster crabs invading spat and older oysters may be due to the difference in amount of water pumped by the host animals.

The ordinary feeding activities of *P. ostreum* were found by Stauber (1945) to be harmful to the host, particularly in causing gill erosions. He described two types of gill damage, *viz.* the small-crab type with a local, sharply delimited erosion of one or more demibranchs, and the large-crab type where an extensive shortening of one or more demibranchs may be seen reaching from the anterior end of the gills to a point usually ventral of the adductor muscle. It is our impression that the gill damage gradually develops from the first type to the other. Nearly all infested oysters show some gill damage. Examination of 1502 oysters, all of the 1955 year class, collected from January 6th to August 1st in 1956 revealed that about 50% had light gill damage, about 40% had moderate gill damage, about 9% had heavy gill damage, and only about 1% had no discernible gill damage. Among older oysters we found a few extreme cases of heavy gill damage where there was hardly anything left of the gills, and such oysters were usually also very poor in condition.

Since the gill damage, as shown by Stauber, interferes with the feeding mechanism of the oyster, and since the crab feeds on food strained from the water by its host, the presence of a crab might be expected to interfere with the growth and reproduction of the host. Overcash (1946) studied quantitatively the condition of Virginia oysters. Employing an index based on the dry weight of the meat in relation to the volume of the shell cavity, she found that infested oysters were

definitely poorer in condition, on the average, than oysters without *Pinnotheres*. Experimentally it has been shown by Egami (1953) that removal of gill tissue in the Japanese oyster, *Crassostrea gigas* causes a decrease in growth rate.

During the present studies the lengths of all infested as well as uninfested 1955 oysters collected on certain sampling dates in 1956 were measured to check for any possible differences in growth rate. The results are presented in Table V, and show no indication of any differences. However, the data pertain only to the possible effect on the oysters' first year of growth, a period in which it could only have harbored a mature crab for about 10 weeks or less. Furthermore, the data do not give any information on possible differences in increase of shell thickness or weight of the living tissues, a fact which should be considered since the correlation between shell and tissue growth is still obscure (Korringa, 1952). Very possibly only the presence of a mature crab over a longer period of time will interfere noticeably with the growth of the host under normal environmental circumstances.

Awati and Rai (1931) presented some very interesting data on the effect caused by *Pinnotheres* sp. on the sex ratio in populations of *Ostrea cucullata* in Indian waters. Among 794 uninfested oysters there were 41.7% males, 56.4% females,

TABLE V
Comparison of mean shell length of infested and non-infested
1955 oysters on the Bay Shore Channel Bed

Date of collection	Number of infested oysters	Number of non-infested oysters	Mean length in mm. of infested oysters	Mean length in mm. of non-infested oysters
6-1-56	120	48	19.1	19.1
5-6-56	103	91	24.3	26.0
6-7-56	116	166	34.3	34.7
26-7-56	118	239	41.6	41.6
12-9-56	54*	125*	49.2	49.7

* Infestations of these oysters with the 1956 year-class of crabs were not considered.

and 2.9% hermaphrodites, while in 86 infested oysters there were 82.6% males, only 10.4% females, and 7.0% hermaphrodites. Since females could be induced to change sex in the laboratory by simple starvation, the authors concluded that the pea crab probably interferes with the food intake of the oyster enough to induce it to produce sperm instead of the more "expensive" eggs.

It would be of interest to know whether the sex ratio is also affected in the American oyster. The genus *Crassostrea* does not exhibit frequent, normal sex changes as does the genus *Ostrea*, but, nevertheless, it has a strong tendency towards protandric hermaphroditism, and the sex ratio is definitely influenced by environmental conditions (Amemiya, 1929; Coe, 1934). Further, Amemiya (1935), and also Egami (1953) have shown experimentally that removal of part of the gill tissue in groups of *Crassostrea gigas* causes the proportions of males to females to rise during the breeding season, if the operations are performed no later than the previous October. There is therefore reason to believe that the reproductive system of *Crassostrea virginica* may be affected by the oyster crab, at least in the second spawning season in which it harbors the same crab, i.e., yearling oysters are probably never affected. This conclusion is also supported by the findings of Berner (1952) who

examined the gonadal condition of more than 300 *Mytilus edulis* infested with *P. pisum*. He found that a partial or even a complete cessation in the production of sexual products often occurred in mussels containing a crab measuring 10 mm. or more in carapace width, but that mussels containing a smaller crab very seldom seemed to be affected. And according to the same author there can be no doubt that the larger crabs were all in their second or third year.

DISCUSSION

Of primary interest in this study of *P. ostreum* was the revelation that both sexes invade their host in the first crab stage, which has become morphologically adapted for its dual role of swimming about in search of a host and of entering it. Further, that about four more, hitherto undescribed, growth stages follow this stage before the crab moults into what was until now thought to be the invasive stage, *viz.* the hard stage.

Since the crab is found in an animal that has been the subject of more research than most marine invertebrates, it may well be wondered why the presence of these early stages has so far been overlooked. There are, however, many reasons for this. They are not found throughout the year. In fact, in fast growing spat and in yearlings and older oysters they may develop into the hard stage within a few weeks. Under all circumstances many of them will soon reach a pre-hard stage in which, if at all possible, it takes more than a casual observation to distinguish them from second stage crabs. The firmly established belief that the hard stage was the invasive stage is in itself another explaining factor. Moreover, the small size and often concealed position of the early stages in all parts of the water conducting system of the host makes them easy to overlook. A careful microscopical examination of the oyster tissues is indeed necessary to find all crabs present.

It is well known that other species of *Pinnotheres* are found in a large number of common intertidal or littoral host animals all over the world, except in arctic and antarctic waters. In spite of this, no developmental stages, equivalent to the invasive or the pre-hard stages of *P. ostreum*, have been taken and recognized as such in nature. It is therefore of considerable interest to discuss the general conclusions concerning the life-history and biology of species of *Pinnotheres* that may or may not be drawn from a study of the literature and the results of the present work. In addition, some information from recent studies on *P. pisum* in Scandinavian waters will also be utilized although the materials and methods as well as the detailed results are not published yet.

More than one hundred species of *Pinnotheres* have been described (Rathbun, 1918; Tesch, 1918; and others), and they are doubtless all either commensals or parasites. This is well established for the large majority of the species, but in some cases no reference is made to a host for a particular species. In most of these cases, however, it can be ascertained that the author's material consisted of hard stage crabs, usually only males, and the collection of this stage free in the water obviously does not mean that the species concerned is free-living. In other cases the original collector has not bothered to note from which host the crab or crabs were taken.

Most of the species inhabit bivalves while a few are found in polychaete tubes, gastropods, holothurians, and tunicates. The majority of them are also known to

occur in more than one host. Many have been taken from half a dozen different bivalves or more (Sakai, 1939; and others), and a few are even known to occur in widely different types of hosts. For instance, *P. maculatus* has been collected both from bivalves and *Chaetopterus* tubes, and *P. pinnotheres* occurs in bivalves as well as tunicates. One of the few species that may be host specific is *P. placunae* described by Hornell and Southwell (1909) which seems to be morphologically adapted to inhabit *Placuna placenta*, a bivalve with closely approximated valves. *P. ostreum* also occurs in other bivalves than *C. virginica* as it has been found in *Pecten* sp. by Ortmann (Gerstaecker and Ortmann, 1901), and on one occasion in *Anomia simplex* by the present authors.

Once the female oyster crab has developed beyond the hard stage it never leaves the host. During the many years of biological work on the Delaware Bay oyster beds, no mature or other post-hard crabs have ever been collected outside a host. We have found dead and dying oysters (gapers) containing post-hard, usually fifth stage crabs, some of which were also dead. It may be that neither the live nor the dying oyster open enough to enable the crab to crawl out. We are, however, convinced that a post-hard crab would not leave a live oyster even if it had an opportunity to do so, and this probably applies to all *Pinnotheres*-host associations. It is certain that adult females of species living in worm tubes, holothurians, and tunicates are unable to leave their host as is evident from the papers by Semper (1881), Enders (1905), Wells (1928, Fig. 76), Tu (1938) and others. The same must be true for those species which live in burrowing and boring bivalves. They can only be entered or left through the siphons which are not wide enough to admit the passage of a mature female. Wells (1940) has some data on this problem for other genera of pea crabs, but his results seem somewhat contradictory to one another. On the other hand, Tu (1938) writes that he has often seen *P. affinis* leave and re-enter the scallop, *Pecten hastatus*?, and Berner (1952) states that all stages except the larger ovigers of *P. pisum* freely change from one host to another. It is not clear, however, whether Tu's observations apply to the post-hard stages, and Berner's statement seems to be based more on opinions than on actual observations. In contrast to Berner, Thompson (1835) emphasizes that although he made extensive dredgings with fine nets, and at all seasons, on grounds with infested mussels he never found a free-living female *P. pisum*.

The species may of course vary in this respect, and it is obvious that some species of host animals would be easier to leave and enter than others. However, since the mature female with its soft-shelled carapace and feeble walking legs seems entirely unadapted for even a temporary stay outside a host, more convincing evidence seems needed to accept Tu's and Berner's statements. These crabs are only able to move slowly and they would be easy prey for any predators. They often lie on their backs on the aquaria floors as well as inside their host, and this is obviously a dangerous habit unless the crab is in a protected position. It may also be asked why two different stages, both specialized for swimming and entering the host, should have developed if all stages could freely move from host to host. In this connection we cannot accept Berner's view that the softness of the carapace facilitates the invasion of the host since even the smaller, specialized hard-stage crabs may be trapped and severely damaged between the valves (Orton, 1921). It is very possible, however, that some or all species inhabiting bivalves that gape upon death may leave their host under such circumstances. This was observed by Wells

(1940) for some other genera of pea crabs, but in view of the above we find it doubtful whether a post-hard *Pinnotheres* would succeed in finding and entering another host.

There can hardly be any doubt that all species of *Pinnotheres* invade their host in the first crab stage. Pre-hard stages must exist in all of them as evidenced by the large size of the hard-stage crab in the many species in which this stage is known, viz. all the species of which the male has been described. It is also reasonable to assume that they are soft-shelled and without swimming hairs as we have found for both *P. ostreum* and *P. pisum*, and that they are therefore not adapted either for a free-living existence or for invading the host. Hence the crab must invade its host either as a megalopa or in the first crab stage as we can safely disregard Semper's (1881) suggestion of the invasion taking place in the zoeal stage. Since it is now known that the two species mentioned above invade their host in the first crab stage, and since this stage of the only other *Pinnotheres* in which it is known, viz. *P. taylori*, described by Hart (1935), closely resemble the other two in having long, plumose swimming hairs on the third and fourth pairs of pereopods, there is every reason to expect this to be the invasive stage in all the species. Consequently we do not agree with Atkins (1954, 1955), who suggested that *P. pinnotheres*, but not *P. pisum*, possibly invades its host in the megalopa stage. Atkins draws attention to a paper by Wells (1940) who found the megalopa of two different species of *Pinnira* inside their bivalve hosts. This genus differs, however, from *Pinnotheres* in many respects as is also indicated by its systematic position in a different subfamily, and the only known first crab stage of this genus, viz. that of *P. sayana*, described by Faxon (1879), apparently does not possess plumose swimming hairs. It seems more significant that Wells never found the megalopa of *Fabia subquadrata*, a species closely related to *Pinnotheres*, although he examined a large number of the bivalves in which this species commonly occurs.

From the above account it follows that neither the male *Pinnotheres* nor the immature females are free-living as so often stated in the literature (Rathbun, 1918; Orton, 1921; Berner, 1952; and others). The free-swimming period of the male during the copulatory period may vary in length for the different species, but it is, nevertheless, only a phase in the otherwise commensal or parasitic life of the crab.

In some species, however, the young invasive stage crabs may invade a host in which they do not occur as adults, and in these cases both sexes migrate from the initial to the final host upon reaching the hard stage. This has been shown to be the case in *P. pisum*, which apparently exhibits a regular host change, the invasive and pre-hard stages having been found only in the clam, *Spisula solida*. Most probably these stages will also be found in other bivalves of the same type, but only the hard-stage crabs may be found in the initial as well as the final host species. Other *Pinnotheres* with a host change should probably be looked for among those species of which free-swimming hard stage females have frequently been taken.

Thus, the specialized hard stage, which primarily has evolved to serve the purpose of uniting the two sexes for copulatory activities, may also serve another important function. Under certain conditions it is also conceivable that females of species which do not normally change host may do so, but in such cases no change of host species needs to be involved. If a number of female oyster crabs invade the same host during the same invasive season, only one will reach the mature stage within that particular oyster (Stauber, 1945). Excessive females therefore either

perish or migrate to other oysters. As discussed earlier, mortalities involving all crabs but one usually take place in spat, but this is not the case in yearlings and older oysters. In fact, Stauber (1945, and unpublished data) found a very large number of older oysters containing 10 or more immature, mostly hard stage crabs in early winter. It therefore seems very possible that the excessive females may survive the winter within the host and migrate to other, non-infested oysters the following spring.

The puzzling occurrence of soft-shelled male *P. ostreum* as large or larger than hard-stage males has been touched upon earlier. Since only few soft-shelled males were found after the mass development of pre-hard crabs into the hard stage in June and the first half of July in 1956 (Fig. 5), we became at first convinced that they were normal pre-hard crabs delayed in their development, especially since the evidence derived from other field data, as well as from the moulting experiments, supported this conclusion. However, while all these data certainly show that hard-stage males do not normally moult into soft-shelled crabs, the recent studies on *P. pisum* indicate that a specimen may now and then do so. If, namely, the preliminary results are correct with regard to the mentioned regular change of host, pre-hard crabs should not occur in host species that act as host for the adult crab, yet soft-shelled males have been taken from *Mytilus edulis* by several authors, including Atkins (1933). It is significant, however, that only very few have been taken while the hard stage has been taken in large numbers. Nevertheless, unless the crab occasionally enters the normal final host already while in the invasive stage, these soft-shelled males must derive from hard-stage crabs, and there are reasons to believe that the latter hypothesis is true. The conspicuously large soft-shelled males of *P. ostreum* usually occur in late summer, and although Atkins (1933) made collections throughout the year, she found two of her soft-shelled specimens on June 6th and the remaining six in early August, *i.e.* in both species they seem to occur mainly after all the pre-hard males should have developed into the hard stage. This poses the still unanswered question as to what may cause such abnormal moultings. Atkins (1933), who did not know about the existence of the soft-shelled pre-hard stages, also wondered about this. She dispelled the statement of Mercier and Poisson (1929) that they were caused by a parasitic isopod, and she found no other parasites in the eight specimens examined by her. As Atkins is a known authority on parasites of *Pinnotheres* it is most unlikely that any were overlooked. One possibility which deserves attention is whether a tendency toward protandric hermaphroditism might be involved since it seems to be the only other factor that could explain the moulting of hard-stage males into a soft-shelled stage very much like the female second stage. An examination of the gonads of freshly caught specimens might help to solve the problem.

Orton (1921) discovered that the female *P. pisum* copulates precociously, and this has been confirmed for *P. ostreum*. However, since the two sexes develop through exactly the same stages until and including the (hard) stage in which the copulation takes place, this is evidently also true for the male. In other words, post-hard males, equivalent to the existing female stages, probably existed somewhere in the line of evolution. When they were no longer needed for the survival of the species they disappeared. There can be little doubt that these phenomena are the results of evolutionary adaptations to the commensal or parasitic life of the genus. The ability of copulating in the hard stage, together with the added adaptations of

this stage for swimming and entering a host, makes it possible for the two sexes to inhabit different host specimens except when mating takes place. And due to the small size and shortened life of the male, the available space and food in the host population is most effectively utilized by the crab population, *viz.* for the vital production of eggs, the number of which is highly dependent on the number and size of the crabs producing them.

In summary it may be said that *Pinnotheres* seems more adapted to its mode of life than hitherto believed, and the genus must have a long evolutionary history behind it. The post-planktonic developmental cycle with its specialized stages, as well as the reproductive biology, is unique and quite unlike anything known from free-living crabs.

The very considerable differences which exist in the development, morphology and biology of pinnotherid crabs make it difficult to judge on which points some of the present findings may also apply to certain other genera. Even within the genus *Pinnotheres* itself there are notable differences, especially with regard to the larvae, a fact which has made Lebour (1928) and others wonder whether they could all belong to the same genus. In short, both from a systematic and biological point of view the pea crabs offer a promising field of research.

SUMMARY

1. It is shown that *Pinnotheres ostreum* invades its host, *Crassostrea virginica* in the first crab stage and not in the hard-shelled stage as hitherto believed.

2. The finding of the first crab stage both in plankton samples and inside oysters marks the first find in nature of this stage for any pinnotherid crab.

3. A preliminary description is given of the following *pre-hard* stages, which were the last unknown stages in the developmental cycle of *P. ostreum*. Both sexes of these stages were found only in the oyster and are never free-living. A full life-history of a pinnotherid crab is now known for the first time.

4. Invasion of the oyster in Delaware Bay takes place in late summer at a time when most of the oyster spat have grown sufficiently large to harbor one or more crabs.

5. More crabs invade spat than yearlings and older oysters, but the survival rate is higher for crabs invading the latter groups of oysters.

6. The growth rate of the crab from the invasive to the mature stage is shown to be positively correlated with the growth rate of the host.

7. Development of the crab is not retarded in slow-growing oysters to the same extent as the rate of growth. This results in a considerable size variation of female crabs just moulted into the mature stage, *viz.* from 4.4 to about 9.0 mm. in carapace width.

8. The *hard stage*, hitherto believed to be the invasive stage, is shown to be a specialized stage which primarily serves the purpose of uniting the two sexes for copulatory purposes. The males leave their hosts in this stage to search for females in other oysters, but this free-swimming period is only a phase in the otherwise parasitic life of the crab.

9. It is shown that males do not develop beyond the hard stage. They disappear shortly after copulation with one or more females, which usually takes place in late

June and in July. In contrast to the females they therefore only become one year old or less.

10. Females become ovigerous in their first summer but do not reach maximum size before their second summer. At least some of them become three years old.

11. Ovigerous crabs are found in Delaware Bay from early June to middle October with a distinct maximum occurring between late July and late August. The older crabs deposit eggs before the one-year-old crabs. The eggs are carried from three to five weeks, and the length of the larval period is three to four weeks.

12. The possible influence of *P. ostreum* on the growth and reproduction of the host is discussed. It is believed that the crab exerts no (discernible) influence in its first year but that it probably does in many cases in its second (and third) year.

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